AALENIAN *TMETOCERAS* (AMMONOIDEA) FROM IBERIA

Taphonomy and Palaeobiogeography

S. R. Fernández-López,[1] M. H. Henriques,[2] A. Linares,[3] J. Sandoval,[3] and M. S. Ureta[1]

[1]Dept. y UEI de Paleontología
Facultad de Ciencias Geológicas (UCM) e Instituto de Geología Económica (CSIC-UCM)
28040-Madrid, Spain
[2]Dept. Ciências da Terra
Centro de Geociências
Universidade de Coimbra
3049-Coimbra Codex, Portugal
[3]Dept. de Estratigrafía y Paleontología
Facultad de Ciencias
Universidad de Granada
18071 Granada, Spain

Abstract

From different areas of the Iberian Peninsula more than 600 specimens of Aalenian *Tmetoceras* have been found. This taxonomic group represents less than 20% of the whole ammonoids recorded in Opalinum, Murchisonae, Bradfordensis and Concavum biozones. *Tmetoceras* representatives, as well as Phylloceratina and Lytoceratina, were more frequent in shelfal basins than in epicontinental platforms. Taphonomic data suggest a eudemic character of the representatives of *T. scissum* in shelfal basins or oceanic areas. Exceptional immigrants and drifted shells of this species arrived in shallow environments of neighbouring platforms. In contrast, representatives of *T. regleyi* inhabited preferentially shallow environments of epicontinental platforms.

T. scissum was a pandemic species, inhabiting oceanic or shelfal environments in the early Aalenian. However, some species of *Tmetoceras,* such as *T. regleyi* and *T. flexicostatum,* were geographically restricted in very distant areas. T. *regleyi* has been found only in Euro-

pean areas of the West Tethyan Subrealm. A pattern of adaptive radiation may have taken place in the Western Tethys during the Opalinum-Murchisonae biochrons, giving rise to *T. regleyi* from *T. scissum*. Specialized forms of *Tmetoceras* (k-strategists such as the individuals of the species *T. regleyi)* are widespread in the epicontinental platforms around the Western Tethys during the Murchisonae and Bradfordensis biochrons. Epicontinental, specialized forms of *T. regleyi* suffered extinction in the latest Bradfordensis Biochron. Shelfal or oceanic, generalist forms of *T. scissum* disappeared in the Western Tethys or the Mediterranean Province in the latest Bradfordensis Biochron, but they survived in the East-Pacific Subrealm.

1. INTRODUCTION

The subfamily Tmetoceratinae is a monogeneric group, *Tmetoceras* (M+m), comprising several European forms distinguished at specific level on the basis of morphological differences: *T. scissum* (Benecke, 1865), *T. regleyi* (Dumortier, 1874), *T. difalense* (Gemmellaro, 1886) and *T. hollandae* (Buckman, 1892). However, when fossils are abundant, these species all appear to intergrade (cf. Callomon and Chandler, 1994).

The main purpose of this paper is to show that the distribution of *Tmetoceras* shells around the margins of the Iberia during the Aalenian was influenced by biogeographical and taphonomic dispersal, related to changes in the relative depth of sea level.

2. TAPHONOMIC CHARACTERS AND DISTRIBUTION OF AALENIAN TMETOCERAS IN IBERIA

More than 600 specimens of Aalenian *Tmetoceras* found *in situ* in different areas of the Iberian Peninsula have been studied (Figure 1). These specimens have been found in the following areas and outcrops:

1. N Lusitanian Basin (Cabo Mondego, Coimbra and Degracias; cf. Perrot, 1955; Mouterde *et al.*, 1964, 1980; Rocha *et al.*, 1981; Henriques, 1989, 1992, 1995).
2. Asturias (Santa Mera and El Puntal; cf. Suárez-Vega, 1974; Fernández-López and Suárez-Vega, 1980).
3. Basque-Cantabrian Basin (Camino, Castillo Pedroso, Cillamayor, Rebolledo de la Torre and San Andrés; cf. Fernández-López *et al.*, 1988b; Goy *et al.*, 1990; Canales *et al.*, 1993).
4. NE Cameros (Préjano and Muro de Aguas; cf. Goy and Ureta, 1981; Ureta, 1985, 1988).
5. NW Iberian Basin (Canales de la Sierra, Castrovido, Hontoria, Rabanera, Talveila and Villavelayo; cf. Ureta, 1985; Ureta and Goy, 1986; Fernández-López *et al.*, 1988a).
6. Aragonese Platform (Obón and Ricla; cf. Mouterde *et al.*, 1978; Fernández-López and Aurell, 1988; Goy *et al.*, 1988).
7. Tortosa Platform (Coll de Soms, Mas de Rojals, Vall Llarga and Vandellós; cf. Fernández-López and Mouterde, 1985; Fernández-López *et al.*, 1996).
8. NW Castilian Platform (Arcos de Jalón and Fuentelsaz; cf. Goy and Ureta, 1987, 1991; Goy *et al.*, 1994).
9. Central Castilian Platform (Barranco de la Hontanilla, Peracense and Rambla del Salto: cf. Fernández-López and Gómez, 1990a, b).

Figure 1. Areas of Iberia mentioned in text: 1) N Lusitanian Basin, 2) Asturias, 3) Basque-Cantabrian Basin, 4) NE Cameros, 5) NW Iberian Basin, 6) Aragonese Platform, 7) Tortosa Platform, 8) NW Castilian Platform, 9) Central Castilian Platform, 10) SE Castilian Platform, 11) Majorca, 12) External Subbetic Basin, 13) Oriental sector of Median Subbetic Basin, 14) Central sector with condensed sections of Median Subbetic Basin, and 15) Central sector with expanded sections of Median Subbetic Basin.

10. SE Castilian Platform (Ribarroja and Domeño; cf. Fernández-López, 1980, 1985).
11. Majorca (Cúber and Llodrá; cf. Goy and Ureta, 1988; Álvaro *et al.*, 1989).
12. External Subbetic Basin (Cortijo Veteta and Sierra de Gaena; cf. Sandoval, 1983).
13. Oriental sector of Median Subbetic Basin (Sierra de Ricote; cf. Seyfried, 1978; Linares and Sandoval, 1993; García-Gómez *et al.*, 1994).
14. Central sector with condensed sections of Median Subbetic Basin (Cerro Méndez and Río Fardes; cf. Linares, 1979; Hernández-Molina *et al.*, 1991; Linares and Sandoval, 1993; García-Gómez *et al.*, 1994).
15. Central sector with expanded sections of Median Subbetic Basin (Cerro Méndez, Montillana and Sierra de San Pedro; cf. García-Gómez *et al.*, 1994; Linares, 1979; Linares *et al.*, 1988; Linares and Sandoval, 1992, 1993).

These areas of the Iberian Peninsula comprise two separate habitats: epicontinental platforms and shelfal basins. Habitats of epicontinental platform were cratonic areas flooded by shallow marine waters. In contrast, habitats of shelfal basins were situated on the continental shelf showing open marine and oceanic environments.

Two shelfal basins were located in Tethyan and Protoatlantic margins of the Iberian Plate throughout Aalenian time: the Betic and the Lusitanian basins (Figure 2). A set of very shallow epicontinental platforms, the so-called Iberian Basin, was situated between them. Depositional environments of these Aalenian basins varied from those of very shallow outer platform to those of deep basin. Aalenian strata are fundamentally limestones which may attain 85 m thick (Henriques *et al.*, 1996). Ammonoid assemblages of these environments varied from those with a predominance of Phylloceratina and Lytoceratina to those that were mainly Ammonitina. For example, ammonoid assemblages in the Median

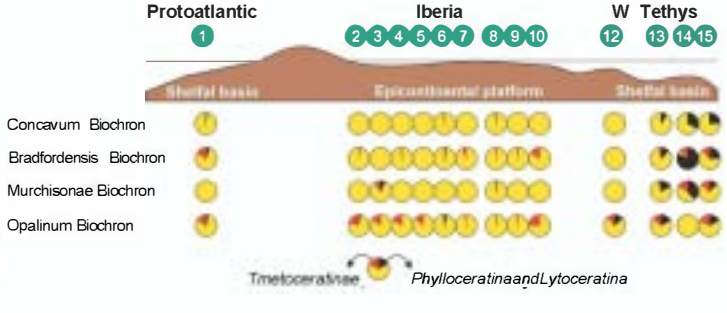


Figure 2. Frequency of Tmetoceratinae and Phylloceratina plus Lytoceratina in different areas of the Iberia during the successive Aalenian biochrons.

Subbetic Basin are dominated by Phylloceratina and Lytoceratina during the Bradfordensis Biochron. In Lusitanian and Iberian basins, Ammonitina are the most frequent Aalenian ammonoids found, and Phylloceratina or Lytoceratina are very scarce. Fossils of *Tmetoceras* are also more abundant in the Betic Basin than in the Lusitanian or in the Iberian basins (Figure 3). The subfamily Tmetoceratinae represents less than 20% of the whole ammonoids recorded in Opalinum, Murchisonae, Bradfordensis, and Concavum biozones. However, from a taphonomic and palaeoecological point of view, the distribution of Aalenian *Tmetoceras* shows conspicuous variations around the Iberian Plate at a zonal scale (Tables 1-4).

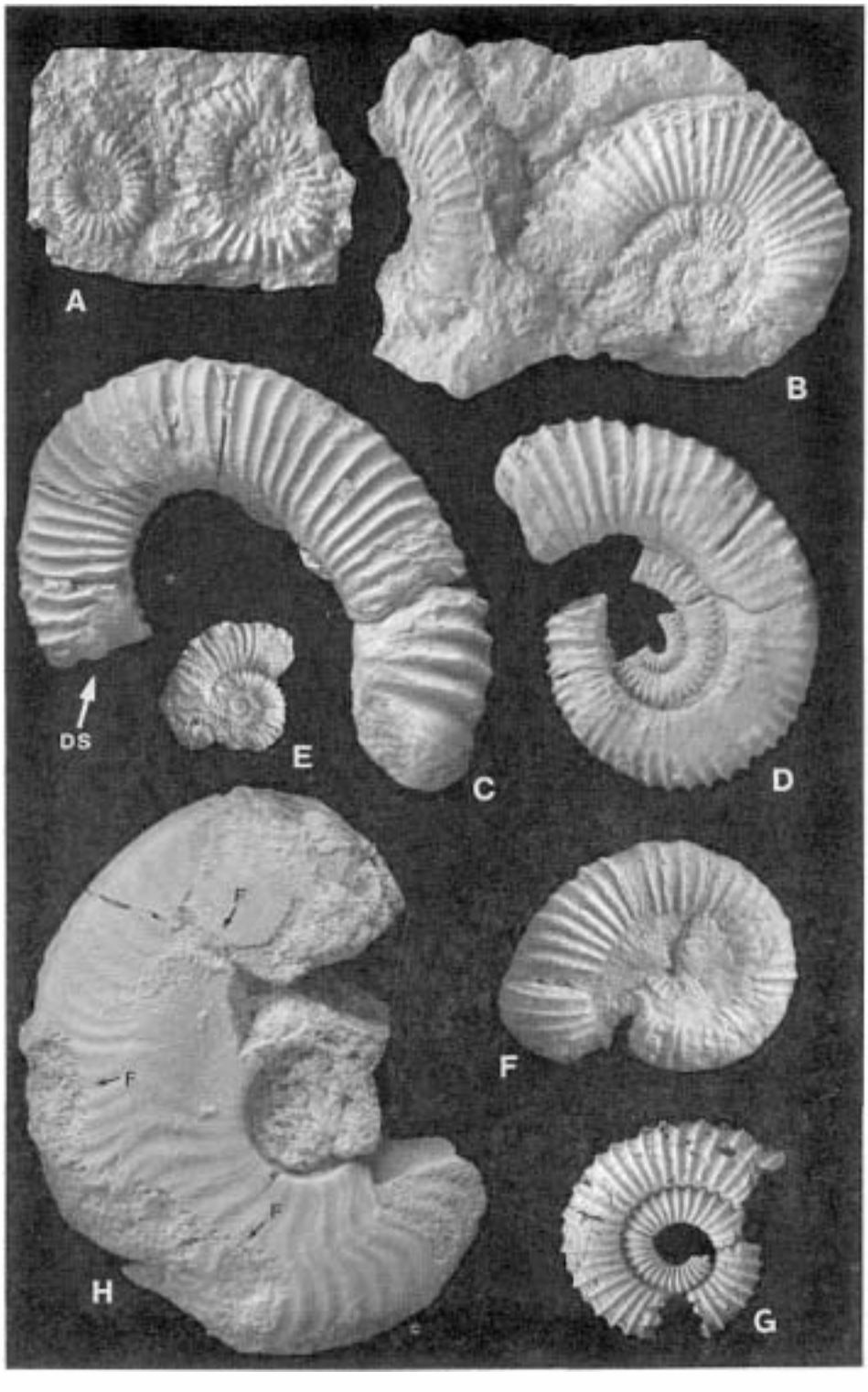
Fragmentary, incomplete specimens are commonly represented among Aalenian ammonoids of the Iberian Peninsula. No accumulated *Tmetoceras* have been identified among them. Fossil assemblages show high degrees of removal *(i.e.,* proportion of resedimented or reelaborate elements). The palaeontological material from Asturias, Basque-Cantabrian and Iberian basins is composed of resedimented or reelaborate elements. They represent individuals with less than 50 mm in diameter. However, Betic and Lusitanian *Tmetoceras* are mostly composed of resedimented specimens showing diameter values between 13 and 78 mm.

Two species of *Tmetoceras* have been recognized: *T. scissum* and *T. regleyi* (cf. Fernández-López *et al.,* 1997). On the basis of morphological criteria, *T. scissum* comprise evolute shells having thin, acute, prominent and distant ribbing, and they have a moderately complex suture line (Fig. 3A-D, F-G). In contrast, representatives of *T. regleyi* are more involute, showing thick, blunt and dense ribs, and their suture line is more simple (Figure 3E).

Specimens of *T. scissum* are more abundant and they have higher stratigraphical persistence in the Betic and Lusitanian basins than in the epicontinental platforms of Iberia (Figure 4). In contrast, specimens of *T. regleyi* are practically restricted to areas of epicontinental platform, where they are the dominant species of the genus during the Murchisonae and Bradfordensis biochrones. Nevertheless, very scarce adult specimens of *T. regleyi* have been found in the Murchisonae and Bradfordensis biozones from the Betic Basin.

Shells of *Tmetoceras* recorded in Aalenian deposits of these areas compose taphonic populations of three types: TP1, TP2 and TP3 (Figure 5). Taphonic populations of type 1

Figure 3. Aalenian *Tmetoceras* of the Iberian Peninsula. (A) Juvenile individuals of *Tmetoceras scissum.* Resedimented elements with complete body chambers. CMB.19.1. Opalinum Biozone. Cerro Méndez (Central sector with expanded sections of Median Subbetic Basin). x2. (B) Post-juvenile individuals of *Tmetoceras scissum.* Resedimented elements with incomplete body chambers. J.RI 1.63.2. Opalinum Biozone. Sierra de Ricote (Oriental, sector of Median Subbetic Basin), x1. (C) Adult individual of *Tmetoceras scissum.* Reelaborated element with complete body showing a disarticulation surface (DS). CM.7.75. Murchisonae Biozone. Cerro Méndez (Central sector with condensed sections of Median Subbetic Basin), x1. (D) Immature individual of *Tmetoceras scissum.* Reelaborated element with incomplete body chamber. CM.A5.20. Murchisonae Biozone. Cerro Méndez (Central sector with condensed sections of Median Subbetic Basin), x1. (E) Post-juvenile individual of *Tmetoceras regleyi.* Reelaborated element with incomplete body chamber. 5SS126/14. Bradfordensis Biozone. Coll de Soms (Tortosa Platform), x1. (F) Post-juvenile individual of *Tmetoceras scissum.* Reelaborated element with incomplete body chamber. PV12/23. Bradfordensis Biozone. Ribarroja (SE Castilian Platform), x1. (G) Post-juvenile individual of *Tmetoceras scissum.* Resedimented element with incomplete phragmocone. SG.107.1. Opalinum Biozone. S. Guião, Degracias (N Lusitanian Basin), x1. (H) Internal mould of a shell of ammonites *(Brasilia)* showing traces of open and lobulate fractures (F) likely produced by crustaceans. Bradfordensis Biozone. Domeño (SE Castilian Platform), x1.


A
B
C
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G
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Table 1. Characters of the Opalinum *Tmetoceras* in different areas of the Iberia

Opalinum Biozone	W LUSITANIAN BASIN	ASTURIAS	BASQUE-CANTABRIAN BASIN	SW CANEDO	NW IBERIAN BASIN	ARAGONESE PLATFORM	CORTONA PLATFORM	NW CASTILIAN PLATFORM	CENTRAL CASTILIAN PLAT.	SE CASTILIAN PLATFORM	MAIORICA	EXTERNAL SUBBETIC BASIN	MEDIAN SUBBETIC BASIN (internal sector)	MEDIAN SUBBETIC BASIN (Central sector, condensed sections)	MEDIAN SUBBETIC BASIN (Central sector, expanded sections)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Specimens of Tmetoceras	»34	»18	23	14	22	4	3	3	1	24	3	6	37	.	150
Frequency	17	20	16	18	12	«1	«1	«1	«1	24	.	13	15	.	21
Fossiliferous levels	34	7	15	5	14	4	3	3	1	1	3	1	5	.	46
Degree of packing	.	61	35	64	36	0	0	0	0	90	0	83	86	.	69
Degree of taphonomic heritage	0	0	0	0	22	0	0	0	0	80	0	85	0	.	0
Incomplete phragmocones (%)	60	98	69	36	37	100	100	100	100	37	33	0	0	.	0
Size-frequency distribution															
uni- (U) or polymodal (P)	U	U	U	.	U	.	.	.	.	U	.	.	U	.	U
asymmetric (A) or normal (N)	N	A	A	.	A	.	.	.	.	A	.	.	N	.	A
negative (-) or positive (+) skew	.	+	+	.	+	.	.	.	.	+	.	.	+	.	+
Shells of juvenile individuals															
absent (A) rare (R) predominant (P)	P	R	.	R	R	.	.	.	.	P	P	R	.	.	R
Shells of adult individuals															
absent (A) rare (R) predominant (P)	R	R	R	.	.	P	P	P	.	R	.	P	R	.	.
Proportion of elements/species	»34	»18	23	14	11	4	3	3	1	20	3	6	37	.	.
Diversity of the genus	1	1	1	1	2	1	1	1	1	1	1	1	1	.	1
Type of ***taphonic population***	TP1-2	TP1-2	TP1-2	TP1-2	TP1-2	TP3	TP3	TP3	TP3	TP1	TP1-2	TP2	TP1-2	.	TP1-2
Frequency of Phylloceratina	0	0	0	0	0	«1	0	0	0	0	.	»10	14	.	13
Frequency of Lytoceratina	«1	«1	0	0	0	0	0	0	0	0	.	»5	4	.	6

Table 2. Characters of the Murchisonae *Tmetoceras* in different areas of the Iberia

Murchisonae Biozone	W LUSITANIAN BASIN	ASTURIAS	BASQUE-CANTABRIAN BASIN	SW CANEDO	NW IBERIAN BASIN	ARAGONESE PLATFORM	CORTONA PLATFORM	NW CASTILIAN PLATFORM	CENTRAL CASTILIAN PLAT.	SE CASTILIAN PLATFORM	MAIORICA	EXTERNAL SUBBETIC BASIN	MEDIAN SUBBETIC BASIN (internal sector)	MEDIAN SUBBETIC BASIN (Central sector, condensed sections)	MEDIAN SUBBETIC BASIN (Central sector, expanded sections)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Specimens of ***Tmetoceras***	.	.	5	.	.	.	.	1	.	.	.	.	1	13	78
Frequency	.	.	9	.	.	.	.	«1	.	.	.	.	2	18	14
Fossiliferous levels	.	.	3	.	.	.	.	1	.	.	.	.	1	3	23
Degree of packing	.	.	40	.	.	.	.	0	.	.	.	.	0	77	70
Degree of taphonomic heritage	.	.	0	.	.	.	.	0	.	.	.	.	0	100	0
Incomplete phragmocones (%)	.	.	60	.	.	.	.	100	.	.	.	.	0	0	0
Size-frequency distribution															
uni- (U) or polymodal (P)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	U
asymmetric (A) or normal (N)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A
negative (-) or positive (+) skew	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Shells of juvenile individuals															
absent (A) rare (R) predominant (P)	.	.	R	.	.	.	.	.	.	.	.	.	.	.	P
Shells of adult individuals															
absent (A) rare (R) predominant (P)	.	.	.	.	.	.	.	.	.	.	.	.	.	P	.
Proportion of elements/species	.	.	5	.	.	.	.	1	.	.	.	.	1	13	39
Diversity of the genus	.	.	1	.	.	.	.	1	.	.	.	.	1	1	2
Type of taphonic population	.	.	TP2	.	.	.	.	TP3	.	.	.	.	TP3	TP2	TP1
Frequency of Phylloceratina	.	.	0	.	.	.	.	0	.	.	.	.	12	30	12
Frequency of Lytoceratina	.	.	5	.	.	.	.	0	.	.	.	.	»6	9	3

Table 3. Characters of the Bradfordensis *Tmetoceras* in different areas of the Iberia

Bradfordensis Biozone	N LUSITANIAN BASIN	ASTURIAS	BASQUE-CANTABRIAN BASIN	NE CANTABRIA	NW IBERIAN BASIN	ARAGONESE PLATFORM	TORTOSA PLATFORM	NW CASTILLIAN PLATFORM	CENTRAL CASTILLIAN PLAT.	SE CASTILLIAN PLATFORM	BALEARICA	EXTERNAL SUBBETIC BASIN	MEDIAN SUBBETIC BASIN (internal sector)	MEDIAN SUBBETIC BASIN (middle sector, condensed facies)	MEDIAN SUBBETIC BASIN (Central Sector, expanded facies)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Specimens of Tmetoceras	»30	.	.	2	.	.	34	3	2	25	.	.	1	1	75
Frequency	17	.	.	2	.	.	3	«1	«1	17	.	.	2	10	10
Fossiliferous levels	15	.	.	1	.	.	3	2	2	1	.	.	1	1	29
Degree of packing	»50	.	.	50	.	.	97	33	0	96	.	.	0	0	61
Degree of taphonomic heritage	20	.	.	0	.	.	0	0	50	100	.	.	0	100	0
Incomplete phragmocones (%)	80	.	.	100	.	.	42	100	100	20	.	.	0	0	0
Size-frequency distribution															
uni- (U) or polymodal (P)	.	.	.	.	.	.	U	.	.	U	.	.	.	.	U
asymmetric (A) or normal (N)	.	.	.	.	.	.	A	.	.	A	.	.	.	.	A
negative (--) or positive (+) skew	.	.	.	.	.	.	+	.	.	+	.	.	.	.	+
Shells of juvenile individuals															
absent (A) rare (R) predominant (P)	.	.	.	.	.	.	P	.	.	P	.	.	.	.	P
Shells of adult individuals															
absent (A) rare (R) predominant (P)	R	.	.	.	.	.	R	P	P	R	.	.	.	.	.
Proportion of elements/species	»30	.	.	2	.	.	34	1	2	25	.	.	1	1	37
Diversity of the genus	1	.	.	1	.	.	1	1	1	1	.	.	1	1	2
Type of taphonic population	TP1-2	.	.	TP1-2	.	.	TP1	TP3	TP3	TP1	.	.	TP3	TP3	TP1
Frequency of Phylloceratina	0	0	0	0	0	«1	0	0	0	0	.	.	8	60	17
Frequency of Lytoceratina	3	«1	0	0	0	0	0	0	0	0	.	.	4	20	8

Table 4. Characters of the Concavum *Tmetoceras* in different areas of the Iberia

Concavum Biozone	N LUSITANIAN BASIN	ASTURIAS	BASQUE-CANTABRIAN BASIN	NE CANTABRIA	NW IBERIAN BASIN	ARAGONESE PLATFORM	TORTOSA PLATFORM	NW CASTILLIAN PLATFORM	CENTRAL CASTILLIAN PLAT.	SE CASTILLIAN PLATFORM	BALEARICA	EXTERNAL SUBBETIC BASIN	MEDIAN SUBBETIC BASIN (internal sector)	MEDIAN SUBBETIC BASIN (middle sector, condensed facies)	MEDIAN SUBBETIC BASIN (Central Sector, expanded facies)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Specimens of *Tmetoceras*	.	.	.	.	.	2	.	2	.	.	.	.	.	.	.
Frequency	.	.	.	.	.	«1	.	«1	.	.	.	.	.	.	.
Fossiliferous levels	.	.	.	.	.	2	.	2	.	.	.	.	.	.	.
Degree of packing	.	.	.	.	.	0	.	0	.	.	.	.	.	.	.
Degree of taphonomic heritage	.	.	.	.	.	100	.	100	.	.	.	.	.	.	.
Incomplete phragmocones (%)	.	.	.	.	.	100	.	50	.	.	.	.	.	.	.
Size-frequency distribution															
uni- (U) or polymodal (P)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
asymmetric (A) or normal (N)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
negative (--) or positive (+) skew	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Shells of juvenile individuals															
absent (A) rare (R) predominant (P)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Shells of adult Individuals															
absent (A) rare (R) predominant (P)	.	.	.	.	.	P	.	P	.	.	.	.	.	.	.
Proportion of elements/species	.	.	.	.	.	2	.	2	.	.	.	.	.	.	.
Diversity of the genus	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.
Type of taphonic population	.	.	.	.	.	TP3	.	TP3	.	.	.	.	.	.	.
Frequency of Phylloceratina	0	0	0	0	0	0	0	0	0	0	0	.	10	30	«5
Frequency of Lytoceratina	2	0	0	0	0	0	0	0	0	0	0	.	0	3	2

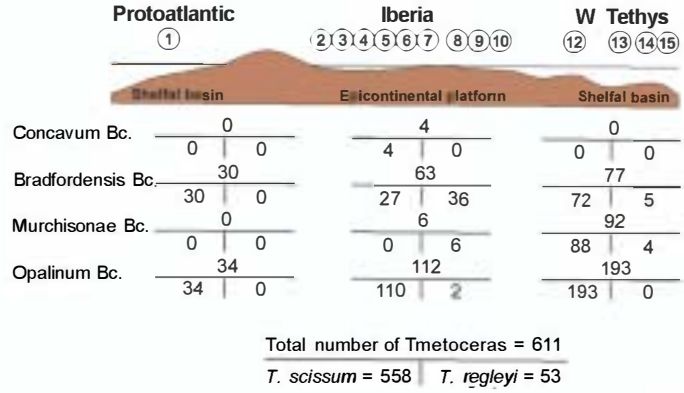


Figure 4. Total number of Aalenian *Tmetoceras* obtained each basin, indicating the specific number of specimens of *T. scissum* and *T. regleyi*.

(TP1) are composed of monospecific shells showing unimodal and asymmetric distribution of size-frequencies, with positive skew. These populations have a high proportion of microconchs and the shells of juvenile individuals are predominant, whilst shells of adult individuals are scarce. Taphonic populations of type 2 (TP2) are composed of mono- or polyspecific shells showing unimodal and normal distribution of size-frequencies, with high kurtosis. Populations of this second type have a low proportion of microconchs and the shells of juvenile individuals are scarce, whilst the shells of adult individuals are common. Taphonic populations of type 3 (TP3) are composed of polyspecific shells showing uni- or polymodal and asymmetric distribution of size-frequencies, with negative skew. Shells of juvenile individuals are absent, microconchs are very scarce and shells of adult individuals are predominant in taphonic populations of this last type.

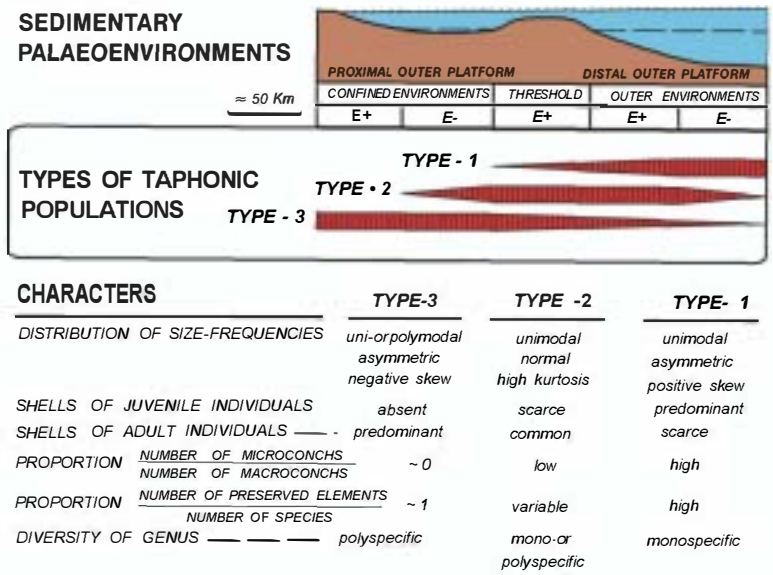
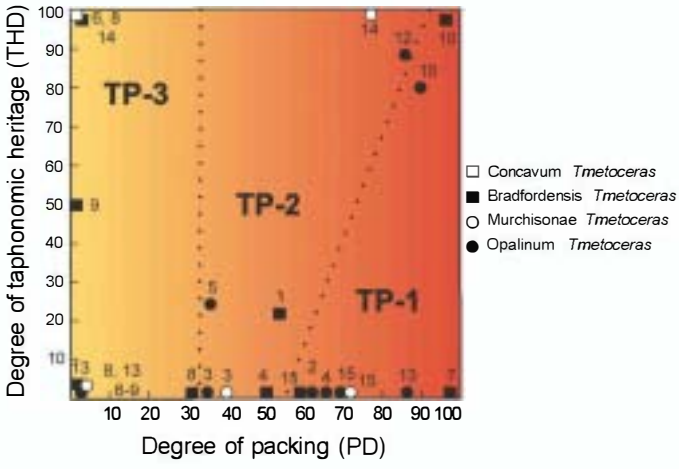


Figure 5. Types of taphonic populations of ammonites developed in environments of shallow outer platform as observed on Middle Jurassic ammonites of the Iberian Basin (after Fernández-López, 1995).



$$PD = \frac{\text{Number of specimens} - \text{Number of fossiliferous levels}}{\text{Number of specimens}} \times 100$$

$$THD = \frac{\text{Number of reelaborated elements}}{\text{Number of specimens}} \times 100$$

Figure 6. Chart showing the different values of packing degree (PD) and taphonomic heritage degree (THD) in the different areas, at a zonal scale, indicating their type of taphonic population (TP-1, TP-2, TP-3).

Different types of taphonic populations of *Tmetoceras* show also distinctive degrees of packing (Figure 6). This index is directly proportional to the abundance of specimens and it takes higher values when the number of fossiliferous levels decreases. Taphonic populations of type 1 have high values of packing (up to 55%). Taphonic populations of type 3 have low values of packing (under 30%). Thus, the degree of packing is another criterion to determine the type of taphonic population. In contrast, the degree of taphonomic heritage, *i.e.* the proportion of reelaborated elements, is not correlated with the type of taphonic population but with the degree of stratigraphical or sedimentary condensation. Taphonic populations of type 1 showing very high degrees of packing and taphonomic heritage were formed in condensed sections from the Median Subbetic Basin during the Murchisonae Biochron, as well as in condensed associations from the External Subbetic Basin during the Opalinum Biochron and from SE Castilian Platform during the Opalinum and Bradfordensis biochrons. Taphonic populations of type 3 showing very high degrees of taphonomic heritage associated with very low degrees of packing were formed in condensed sections from the Median Subbetic Basin during the Bradfordensis Biochron. Some taphonic populations of type 3 displaying very high degrees of taphonomic heritage occur also in condensed associations from Aragonese Platform during the Concavum Biochron and from NW Castilian Platform during the Bradfordensis Biochron.

Opalinum *Tmetoceras* are fairly common in Lusitanian, Iberian and Betic basins (Figure 7). Their frequencies are lower than 1% in the Tortosa, Aragonese and Castilian Platforms. Taphonic populations developed in the Betic and Lusitanian basins, as well as in the deepest environments of the Iberian Basin, were of types 1 and 2. In contrast, taphonic populations were of type 3 in the shallower environments of the Iberian Basin. All the Opalinum *Tmetoceras* found in the Betic and Lusitanian basins are *T. scissum* (Figure 8). However, a post-juvenile specimen of *T. regleyi* has been found in the upper portion of the Opalinum Biozone, associated with abundant specimens of *T. scissum* in the NW Iberian Basin.

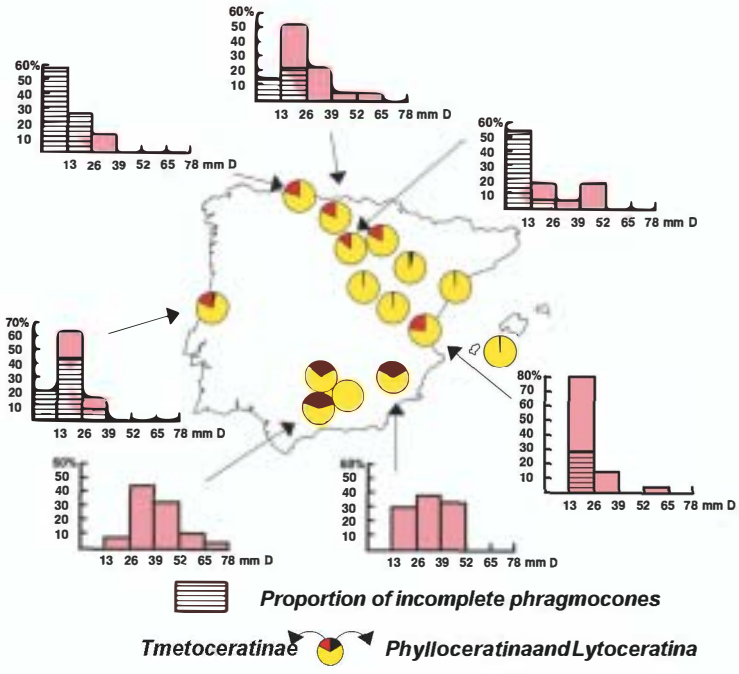


Figure 7. Frequency of Tmetoceratinae and Phylloceratina plus Lytoceratina in different areas of Iberia, and some size-frequency distributions of *Tmetoceras,* from the Opalinum Biozone.

In the Iberian Peninsula, Murchisonae rocks are thin compared with the Bradfordensis rocks above or with the Opalinum below. Murchisonae ammonites are also more scarce. Specimens of *Tmetoceras scissum* are frequent in some Betic outcrops only, and they correspond mainly to monospecific taphonic populations of type 1 (Figure 9). *Tmetoceras* recorded in the Murchisonae Biozone of the Basque-Cantabrian Basin comprise local polyspecific assemblages (Figure 10). A few specimens of *Tmetoceras scissum* have been obtained from the Basque-Cantabrian Basin, associated with scarce juvenile and post-juvenile specimens of *T. regleyi* that represent probable demic individuals. Some specimens of *T. scissum* founded in the NW areas of the Castilian Platform are adult. A few adult specimens of *Tmetoceras regleyi* have been obtained also from the central sector of Median Subbetic Basin, associated with abundant specimens of *T. scissum.* No Murchisonae *Tmetoceras* are known from the Lusitanian Basin.

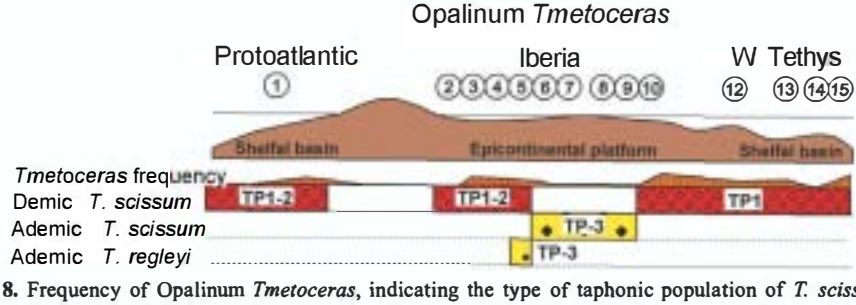


Figure 8. Frequency of Opalinum *Tmetoceras*, indicating the type of taphonic population of *T. scissum* or *T. regleyi* in each area.

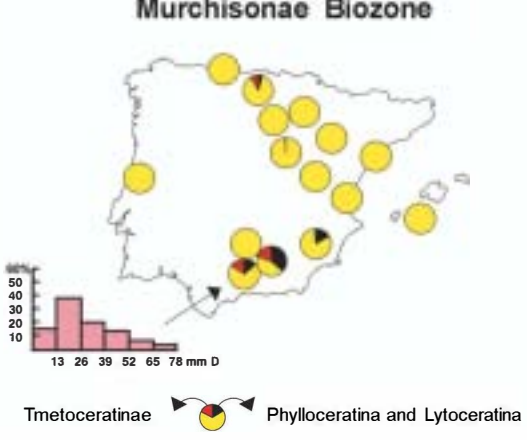


Figure 9. Frequency of Tmetoceratinae and Phylloceratina plus Lytoceratina in different areas of Iberia, and the size-frequency distribution of *Tmetoceras* specimens in the central sector with expanded sections of Median Subbetic Basin, from the Murchisonae Biozone.

Ammonoids are more frequent and widespread in the Bradfordensis Biozone than in the Murchisonae Biozone of Iberia. Bradfordensis *Tmetoceras* are quite frequent in Median Subbetic Basin, Lusitanian Basin and SE Castilian Platform (Figure 11). Taphonic populations of *T. scissum* developed in the Betic and Lusitanian basins, as well as in the SE Castilian Platform, were of types 1 and 2 (Figure 12). In contrast, taphonic populations of *T. scissum* were of type 3 in shallower areas of the Iberian Basin and Betic Basin. However, specimens of *T. regleyi* become relatively frequent in some deep areas of the Iberian Basin, composing taphonic populations of type 1, whilst in the Betic Basin only very scarce adult specimens of this species have been found.

Bradfordensis taphonic populations of *T. scissum* in the SE Castilian Platform, as well as taphonic populations of *T. regleyi* in the Tortosa Platform, show distinctive features (Figure 11). These populations are of type 1 and they display higher proportions of incomplete phragmocones among the largest specimens. These higher proportions of fragmentary shells among the largest specimens is indicative of fragmentation of the shells by predators or scavengers associated with low values of sedimentation rates. Under opposite conditions, with high values of sedimentation rates and showing no evidence of predators or scavengers, the mechanical fragmentation of shells by turbulence produced higher proportions of incomplete phragmocones among the smallest specimens (Fernández-López and Mouterde, 1994: Fernández-López, 1997). The common occurrence of open and lobulate fractures in ammonite shells of these two areas also confirm this interpretation (Figure 3H).

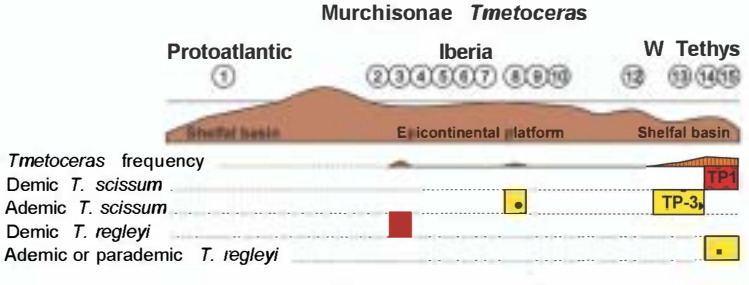


Figure 10. Frequency of Murchisonae *Tmetoceras*, indicating the type of taphonic population of *T. scissum* or *T. regleyi* in each area.

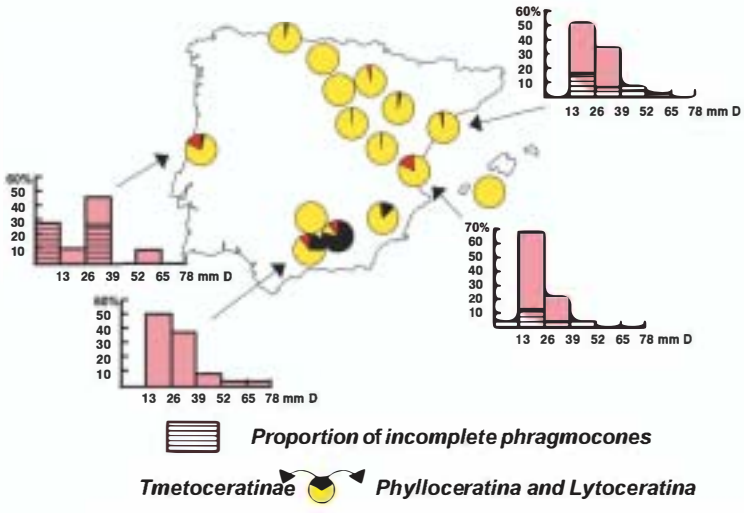


Figure 11. Frequency of Tmetoceratinae and Phylloceratina plus Lytoceratina in different areas of Iberia, and some size-frequency distributions of *Tmetoceras*, from the Bradfordensis Biozone.

Several *Tmetoceras* have been obtained from condensed associations along the Iberian Cordillera in deposits of the upper Aalenian and of the lower Bajocian (Figures 13, 14). These specimens are the only *Tmetoceras* identified in the Iberian Plate in post-Bradfordensis sediments, but they are reelaborate fossils. No Concavum *Tmetoceras* are known from the Lusitanian or Betic basins.

3. PALAEOECOLOGICAL INTERPRETATIONS AND HABITATS

Type of taphonic population, abundance and frequency of specimens, stratigraphic persistence and degree of packing are distinctive criteria in interpreting the palaeoecology and palaeobiogeography of the recorded associations of ammonites. Biogeographical dispersal and necroplanktic drift of shells (a case of taphonomic dispersal) were the main determining factors on the final distribution of the ammonite shells (Figure 15). Consequently, the present distribution of ammonite shells reflect both their original and post-mortem distribution.

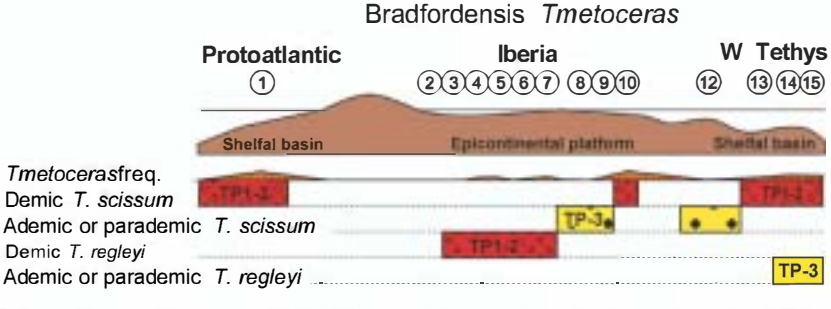


Figure 12. Frequency of Bradfordensis *Tmetoceras*, indicating the type of taphonic population of *T. scissum* or *T. regleyi* in each area.

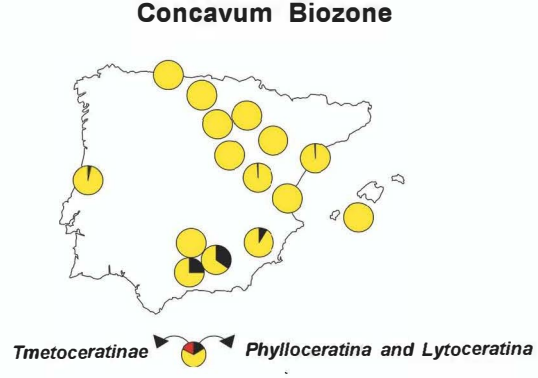


Figure 13. Frequency of Tmetoceratinae and Phylloceratina plus Lytoceratina of the Concavum Biozone in different areas of Iberia.

In Lusitanian and Iberian basins, representatives of Ammonitina are dominant among the Aalenian ammonoids, and the scarce specimens of Phylloceratina or Lytoceratina represent ademic organisms. In Betic Basin, as an area of the West Tethys, Aalenian Phylloceratina and Lytoceratina were represented by demic organisms.

Eudemic *Tmetoceras* are represented in the fossil record by taphonic populations of type 1, characterized by the relative abundance of juvenile elements and high values of taphonomic packing. In contrast, ademic *Tmetoceras* are represented by taphonic populations of type 3, showing low values of taphonomic packing, and they are dominated by adult elements. The active and passive biodispersal led to the occurrence of immigrant and transported *Tmetoceras,* which respectively are miodemic and parademic organisms. Biodispersed *Tmetoceras* are represented in the fossil record by taphonic populations of type 2 or 3 showing median values of taphonomic packing.

Taphonomic data suggest a eudemic character to the *T. scissum* representatives recorded in shelfal basins of the Iberian Plate (Figure 16). Aalenian *T. scissum* are widely distributed in the Betic and Lusitanian basins, where they occur in rich but nearly monospecific associations. Eudemic *T. scissum* inhabited basin areas, characterized by the occurrence of juvenile specimens and taphonic populations of type 1. In contrast, many allochthonous elements of *T. scissum* from the Iberian Basin are interpreted as having arrived at their present locations by necroplanktic drift. The taphonomic dispersal produced the concentration of adult shells of *T. scissum* in shallow neritic environments, representing ademic organisms. They did not breed or ontogenetically develop in the Castilian and Aragonese platforms. In the Castilian Platform, there is evidence of shell transport from the north (Fernández-López and Gómez, 1990a). Northwestwards from Castilian and Aragonese platforms, the NW Iberian Basin, NE Cameros, Basque-Cantabrian Basin and Asturias were the depositional sites of autochthonous and allochthonous shells of *T. scissum* throughout the Aalenian time.

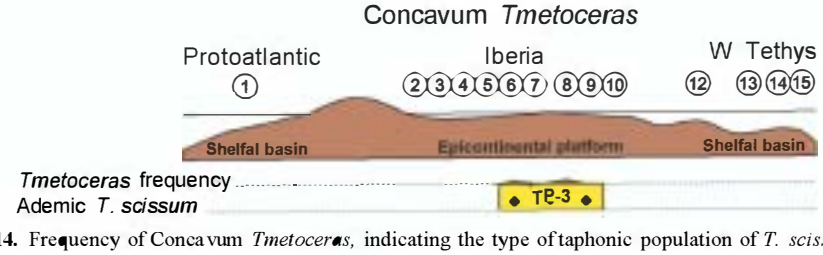


Figure 14. Frequency of Concavum *Tmetoceras,* indicating the type of taphonic population of *T. scissum* in each area.

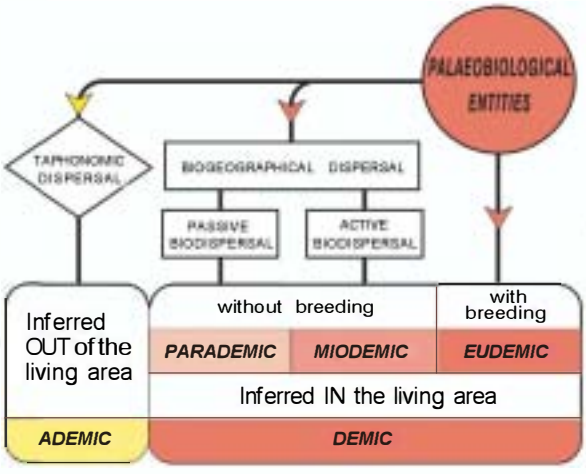


Figure 15. Summary of the palaeobiogeographical categories mentioned in this work. The palaeobiological entities, in particular ammonites, are demic when their remains are found in their living area. Conversely, they are ademic organisms or taxa when they are inferred outside of their living area. Demic species may be inferred in their breeding area (eudemic), in an area normally occupied but where they do not breed (miodemic), or in a living area occasionally reached by passive biodispersal (parademic; after Fernández-López, 1990, 1991 and Fernández-López and Meléndez, 1995).

Some Opalinum specimens exhibiting morphological characters of *T. regleyi* have been found in the NW Iberian Basin, but they are interpreted as post-juvenile, ademic organisms (Figure 17). The active and passive biodispersal led to the occurrence of immigrant and transported *T. regleyi* in the Iberia, which respectively represent miodemic and parademic organisms. The active biodispersal led to the occurrence in outer platforms of immigrant *T. regleyi,* which represent miodemic organisms, during the Murchisonae Biochron. Taphonic populations of *T. regleyi* dominated by juvenile individuals were produced by eudemic organisms in the Iberian Basin during the Bradfordensis Biochron. Scarce adult specimens of *T. regleyi* confined to isolated horizons in the Betic Basin are interpreted as evidence of parademic organisms dispersed during the Murchisonae and Bradfordensis biochrons.

In conclusion, shells of Aalenian *Tmetoceras* have been accumulated in widely distributed areas throughout the Iberian Plate during the Opalinum Biochron. However, the taphonomic and biogeographical dispersal of *Tmetoceras* through the Iberian Basin was hindered during the Murchisonae Biochron, as a consequence of the relative fall of sea level. A new relative rise of sea level during the Bradfordensis Biochron favoured the immigration ofjuvenile *Tmetoceras* in the deepest areas of the epicontinental platforms. Se-

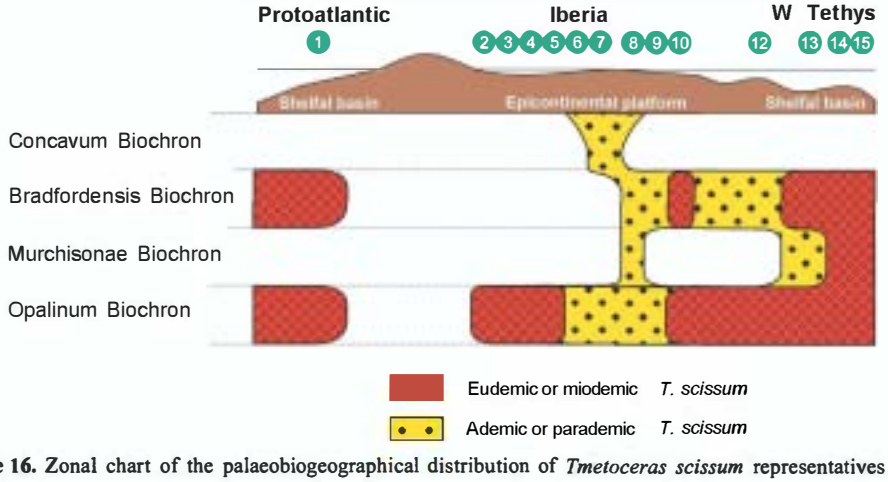


Figure 16. Zonal chart of the palaeobiogeographical distribution of *Tmetoceras scissum* representatives in the Iberia.

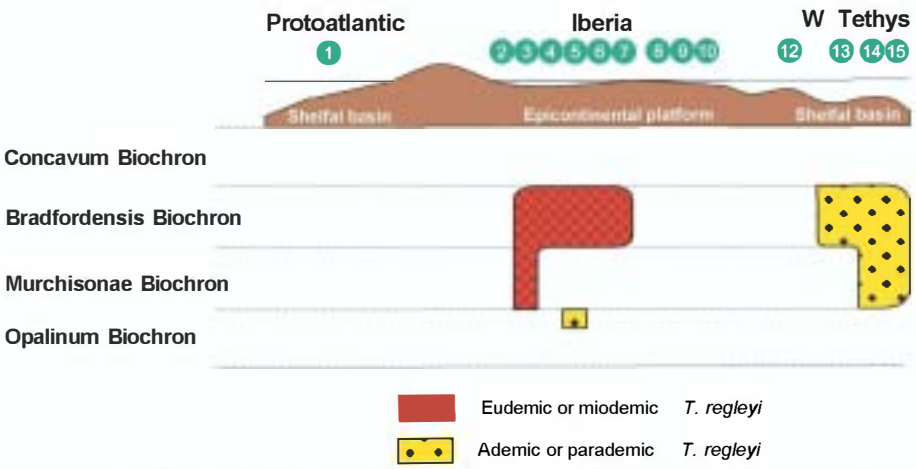


Figure 17. Zonal chart of the palaeobiogeographical distribution of *Tmetoceras regleyi* representatives in the Iberia.

veral specimens of *Tmetoceras* have been found in the rocks of the Concavum Biozone, but they are reelaborate elements derived from older sediments. The Iberian Basin was not active as an epicontinental migration route for Aalenian *Tmetoceras*. *T. scissum* inhabited environments of shelfal basins. *T. regleyi* inhabited environments of epicontinental platforms. However, *T. scissum* occurs together with *T. regleyi* in beds of the Iberian and Betic basins. These two species appear to intergrade, but they were ecological and biogeographically differentiated. Several lines of taphonomic evidences (such as type of taphonic population, abundance, frequency, stratigraphic persistence, degree of packing, and degree of taphonomic heritage) support the concept that the environments of outer epicontinental platform were the sites inhabited by *T. regleyi*.

4. GLOBAL DISTRIBUTION OF TMETOCERAS

Tmetoceras can be considered a pandemic genus of ammonites abundantly represented in the northern margins of the West Tethyan Subrealm, from north Africa and western Europe eastwards to southeast Asia and beyond, and around the Pacific Ocean, including the East-Pacific Subrealm (Figure 18). Although no abundant Aalenian *Tmetoceras* are known from the Arctic Province, some species have been found in Alaska (Westermann, 1964, 1981, 1992). Aalenian *Tmetoceras* occur in the following two provinces of the Boreal Realm: the Bering Province (North Pacific margin and northwestern North America; cf. Imlay, 1955, 1962, 1964; Poulton, 1982; Poulton and Tipper, 1991; Poulton *et al.*, 1991) and the Sub-Boreal Province (Scotland, northern France, northern Germany, Poland; Morton, 1965; Bielecka *et al.*, 1970; Morton and Hudson, 1995).

Specimens of *T. scissum* have been found in the following three provinces of the West Tethyan Subrealm:

1. Northwest European Province (northwestern areas of the Iberian Basin, Britain, northern France, Germany, Rumanian Carpathians; cf. Buckman, 1892, 1907; Arkell, 1933; Patrulius and Popa, 1971; Dietl, 1977; Dietl and Etzold, 1977; Callomon and Chandler, 1990, 1994; Callomon, 1995).

Figure 18. Palaeogeographical distribution of *Tmetoceras* representatives.

2. Sub-Mediterranean Province (epicontinental seas of North Africa, northern Lusitanian Basin, southeastern areas of the Iberian Basin, southern and central France, southern Germany, Switzerland, Iran, Caucasus; cf. Flamand, 1911; Fischer, 1915; Kakhadze, 1942; Colo, 1961, 1964; Rieber, 1963; Elmi, 1967; Seyed-Emami, 1967; Contini, 1970; Braun and Jordan, 1976; Elmi and Caloo, 1985; Benshili, 1989; Rostovtsev, 1991; Westermann, 1992; Elmi and Rulleau, 1994; Rulleau, 1995).
3. Mediterranean (or West Tethyan) Province (shelfal or oceanic areas of North Africa, southern Spain, Italy, Austria, Hungary, Bulgaria; cf. Benecke, 1865; Vacek, 1886; Gregorio, 1886; Gemmellaro, 1886; Ramaccioni, 1934; Maubeuge, 1955; Dubar, 1960; Geczy, 1967; Fischer, 1970; Venturi, 1985; Kälin and Ureta, 1987; Mouterde and Elmi, 1991; Sadki, 1996; Callomon *et al.*, 1995; Cresta, 1996).

T. scissum has been recognized in southern Asia (cf. Sato, 1954; Sato *in* Komalarjun and Sato, 1964; Braun and Jordan, 1976) and in the West Pacific Province (Japan and far eastern of the former USSR; cf. Sato, 1954). Specimens of *T. scissum* have been found also in the following three provinces of the East-Pacific Subrealm:

1. Andean Province (western South America, Chile, Peru, Argentina; cf. Burckhardt, 1903; Westermann and Riccardi, 1972; Bogdanic *et al.*, 1985; Hillebrandt and Westermann, 1985; Hillebrandt *et al.*, 1986; Gröschke *et al.*, 1988; Riccardi *et al.*, 1990, 1992; Westermann, 1992).
2. Athabascan Province (western North America; Frebold, 1951, 1964; Frebold *et al.*, 1969; Imlay, 1982; Poulton *et al.*, 1991; Poulton and Tipper, 1991; Poulton *et al.*, 1992).
3. Shoshonean Province (Western Interior of the United States; Imlay, 1973).

In conclusion, *T. scissum* was a pandemic species, inhabiting oceanic or shelfal environments in early Aalenian. However, some species of *Tmetoceras*, such as *T. regleyi* and

T. flexicostatum, were geographically restricted in very distant areas. *T. regleyi* has been found only in European areas of the West Tethyan Subrealm. Representatives of *T. regleyi* were distributed mainly in the Sub-Mediterranean and Northwest European provinces, inhabiting shallow environments of epicontinental platforms (cf. Dumortier, 1874; Gemmellaro, 1886; Roman and Boyer, 1923; Buckman, 1892; Schlegelmich, 1985; Rulleau, 1995). It is suggested here that a pattern of adaptive radiation may have taken place in the Western Tethys during the Opalinum-Murchisonae biochrons, giving rise to *T. regleyi* from *T. scissum.* Specialized forms of *Tmetoceras* (k-strategists such as the individuals of the species *T. regleyi)* are widespread in the epicontinental platforms around the Western Tethys during the Murchisonae and Bradfordensis biochrons. Epicontinental, specialized forms of *T. regleyi* suffered extinction in the latest Bradfordensis Biochron. Shelfal or oceanic, generalist forms of *T. scissum* disappeared in the Western Tethys or the Mediterranean Province in the latest Bradfordensis Biochron (Fernández-López *et al.,* 1997), but they survived in the East-Pacific Subrealm. In latest Bradfordensis Biochron or in earliest Concavum Biochron, *T. scissum* gave rise to *T. kirki* (Westermann), a species restricted to the East-Pacific Subrealm (Westermann, 1964, 1992; Westermann and Riccardi, 1972; Bogdanic *et al.,* 1985; Hillebrandt and Westermann, 1985; Poulton and Tipper, 1991).

From a palaeobiogeographical point of view, distinctive sedimentary basins of Iberia belonged to three adjacent bioprovinces throughout Aalenian time: Mediterranean, Sub-Mediterranean and Northwest European provinces (Figure 19). The relative orientation of the Iberian Peninsula has been accomplished on the basis of the palaeogeographical data published by Ziegler (1990) and Dercourt *et al.* (1993).

The Mediterranean Province included the Betic Basin and it occupied regions open to oceanic influence, showing characteristically high abundance of Phyllo- and Lytoceratina, where Hammatoceratidae plus Tmetoceratinae were more frequent than Graphoceratidae.

The Sub-Mediterranean Province essentially occupied the epicontinental seas bordering the northern margins of Tethys (cf. Page, 1996); in particular, eastern areas of the Iberian Basin (SE Castilian Platform, Tortosa Platform and Aragonese Platform, at least), but also some regions open to oceanic influence such as the North Lusitanian Basin. In the

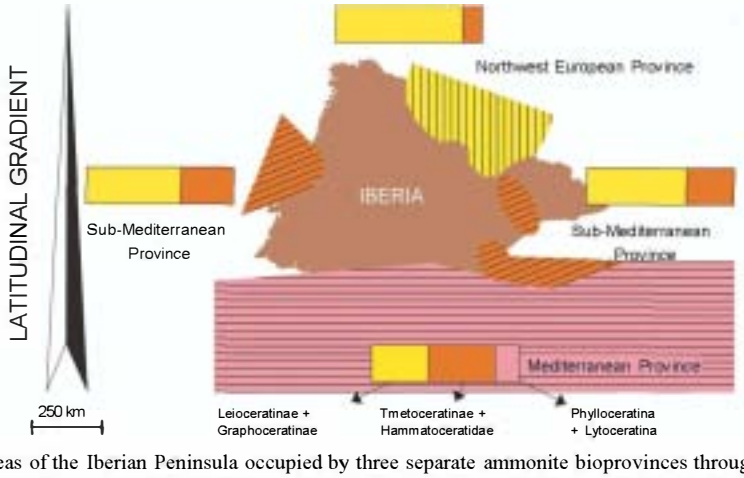


Figure 19. Areas of the Iberian Peninsula occupied by three separate ammonite bioprovinces throughout Aalenian time. NW and Central areas of the Castilian platform were not inhabited by *Tmetoceras,* although some shells arrived to these shallow, epicontinental, outer platforms by nekroplanktic drift. The diversity of ammonoid faunas decrease towards the northern areas, from the Mediterranean Province to the Northwest European Province. This biogeographic gradient was latitudinally limited by environmental factors, including temperature, showing no evidences of a bathymetric control.

Sub-Mediterranean Province, demic Phyllo- and Lytoceratina were generally absent; ademic Phyllo- and Lytoceratina were not important elements of the preserved associations; ammonoid diversity was relatively high; and Graphoceratidae were more frequent than Hammatoceratidae plus Tmetoceratinae. No demic *Tmetoceras* are known from the NW and Central areas of the Castilian Platform.

The Northwest European Province encompassed northwestern areas of the Iberian Basin (Asturias, Basque-Cantabrian Basin and NE Cameras). In this province even ademic Phyllo- and Lytoceratina were generally absent; ammonoid diversity was relatively low; and Graphoceratidae representatives were predominant elements (up to 90%).

The distribution of the Sub-Mediterranean Province in the Iberian Plate (Figure 19), from areas open to oceanic influence of the Lusitanian Basin to areas occupied by shallow epicontinental seas of the Iberian Basin, allows us to exclude a bathymetric control of this bioprovince. The ammonoid provincialism through the Aalenian in these areas may have been latitudinally limited by environmental factors, including temperature rather than depth, since the diversity of ammonoid faunas decrease towards the northern areas.

5. CONCLUSIONS

Tmetoceras scissum and *T. regleyi* appear to intergrade, but they were ecological and biogeographically differentiated. In Iberia at least, populations of *T. scissum* and *T. regleyi* were not coexistent. However, by necroplanktic drift, the shells of these species may be associated in the same sites and beds.

Taphonomic data suggest a eudemic character in shelfal basins or oceanic areas to the representatives of 7! *scissum*. Nevertheless, exceptional immigrants and drifted shells of this species arrived in shallow environments of neighbouring platforms. In contrast, representatives of *T. regleyi* inhabited preferentially shallow environments of epicontinental platforms.

Several taphonomic criteria (type of taphonic population, abundance, frequency, stratigraphic persistence, degree of packing, and degree of taphonomic heritage) support the concept that epicontinental platforms were the sites of adaptive radiation of *T. regleyi*.

The biogeographical dispersal of *T. scissum* and *T. regleyi*, and the arrival of immigrants in the epicontinental platforms of Iberia, were favoured by the relative sea-level rise during the Opalinum and Bradfordensis biochrons. The relative sea-level fall during the Murchisonae and Concavum biochrons decreased the accessibility of *Tmetoceras* shells from shelfal basins to epicontinental platforms. The Iberian Basin was not active as an epicontinental migration route for Aalenian *Tmetoceras*.

The ammonoid provincialism throughout the Aalenian in Iberia may have been latitudinally limited by environmental factors, including temperature, since the diversity of ammonoid faunas decrease towards the northern areas.

The taphonomic interpretation of successive transients is very important in explaining the palaeobiogeographical distribution of species and the diversity of genera. The general conclusion is that taphonomic analysis of successive transients, as in this case, are relevant in interpreting the biogeographical distribution and the taxonomic diversity of ammonites.

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